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Species traits explain long-term population trends of Finnish cuckoo wasps (Hymenoptera: Chrysididae)

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Abstract. 1. Kleptoparasitic and parasitoid insects are expected to be particularly sensitive to changes in habitat availability due to their high trophic position and small population sizes compared with their hosts, but there are only few quantitative studies on their population changes.

2. Here, we studied the distribution and abundance of 48 kleptoparasitic and parasitoid species of cuckoo wasps (Chrysididae) and eight selected host species recorded in Finland from 1840 to 2015 based on an extensive survey of entomological collections. Population trends were assessed by studying changes in occupancy in 10 × 10 km grid squares between two study periods, 1840–1967 and 1968–2015.

3. Statistically significant decreases in occurrence were found for 11 cuckoo wasp species and one host species, while significant increases were not observed for any species. Trends of cuckoo wasps and their hosts were positively correlated, and changes were generally stronger in cuckoo wasps than in their hosts.

4. In a comparative analysis of species traits, abundance, body size and nesting type of host were related to occurrence changes of cuckoo wasps. Scarce and small species that use above ground-nesting hosts declined more than abundant and large species that use ground-nesting hosts.

5. Cuckoo wasp species dependent on dead wood are more vulnerable to changes in the environment than species associated with open sandy habitats. While both groups of species have probably suffered from habitat loss, the emergence of secondary habitats may have benefitted species living in sandy areas and compensated for the negative impact of habitat destruction.

Key words. Declining trend, distribution, host, host–parasitoid dynamics, kleptoparasite, museum collections, occurrence, parasitoid, sun-exposed dead wood, threatened species, vulnerability of high trophic level.

Introduction

Major changes in land use have profoundly altered landscapes and habitats in large parts of the world over the last two centuries. In Europe, particularly the introduction of large-scale industrial forestry and agriculture during the 20th century, including efficient prevention of forest fires and abandonment of traditional animal husbandry, has dramatically transformed the structure of woodlands and agricultural landscapes (Stoate *et al.*, 2009; Paillet *et al.*, 2010). Forests have become more homogeneous and closed with less large trees and dead wood (Kouki *et al.*, 2001), while flower-rich meadows and pastures have disappeared from agricultural areas (Cousins *et al.*, 2015). These changes, in combination with climatic factors, have benefitted some organisms, while others have suffered and even become threatened. In northern Europe, especially species dependent on natural forests (Hyvärinen *et al.*, 2006; Tikkanen *et al.*, 2006) and semi-natural grasslands (Kuussaari *et al.*, 2007) have been negatively affected.

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While population trends of species are often linked to their habitat requirements, also other ecological and life-history traits can affect responses to environmental changes. Niche breadth and dispersal ability can determine insect species' responses to human-induced changes, so that a narrow niche breadth (i.e. a specialised diet) and a poor dispersal ability are predicted to make species more vulnerable (e.g. Kotiaho *et al*., 2005; Bommarco *et al*., 2010; Öckinger *et al*., 2010). Declining trends or increased vulnerability have also been associated with other life-history traits, such as large body size (Bartomeus *et al*., 2013), nest site location (Potts *et al*., 2005; Steffan-Dewenter *et al*., 2006; Williams *et al*., 2010) and solitary or social lifestyle (Steffan-Dewenter *et al*., 2006; Williams *et al*., 2010). Kleptoparasitic and parasitoid species, which require viable host populations, are more vulnerable to habitat loss than species at lower trophic levels (e.g. Komonen *et al*., 2000; Roslin *et al*., 2013), but quantitative studies covering entire insect groups are virtually lacking (Hochberg, 2000; Shaw & Hochberg, 2001).

Cuckoo wasps (Hymenoptera, Chrysididae) are a group of wasps, which develop during their larval stage as kleptoparasites or parasitoids of mainly other hymenopterans (Kimsey & Bohart, 1991). While parasitoids feed directly on the host larva or pupa, kleptoparasites (or brood parasites) mainly utilise the food items stored in the host brood cell (O'Neill, 2001). Both modes of development practically always result in the death of the host. When occasionally more than one host brood cell is destroyed, the kleptoparasite can be also considered to be a predator. Although kleptoparasites mostly feed on the same food as their hosts and may thus be considered as inter-specific competitors (cf. Iyengar, 2008), they share several characteristics in their lifestyle with species belonging to a higher trophic rank, as they are totally dependent on their hosts and therefore comparable with parasitoids. Most North-European species of the subfamily Chrysidinae are kleptoparasites of solitary wasps of the families Vespidae and Crabronidae, whereas a few species are ectoparasitoids of solitary bees of the family Megachilidae. Species of the subfamily Cleptinae are ectoparasitoids of sawfly prepupae of the families Tenthredinidae and Diprionidae (Paukkunen *et al*., 2014, 2015). As the hosts of most cuckoo wasps themselves are highly specialised predators or pollen feeders, which require specific nesting sites and nest building material, cuckoo wasps as their natural enemies are expected to be particularly vulnerable to environmental changes. Many cuckoo wasp species are also highly specialised in their host selection (Pärn *et al*., 2014) and probably have poor dispersal abilities due to their small size (Greenleaf *et al*., 2007; Gunton & Pöyry, 2016).

The sensitivity of cuckoo wasps for environmental changes has become evident in the latest North-European Red List assessments. The proportion of Red-Listed cuckoo wasp species is exceptionally high in all Nordic countries (Paukkunen, 2010; Larsson, 2015; Ødegaard *et al*., 2015). For example, nearly half of the 49 cuckoo wasp species known from Finland (Paukkunen *et al*., 2014, 2015) are considered near threatened, threatened or regionally extinct (Paukkunen, 2010; Table S2). According to such evaluations, the main threat for cuckoo wasps is habitat loss, and especially the decrease of sparsely vegetated dry meadows and biotopes with sun-exposed dead wood.

Despite Red List assessments indicating severe declines in cuckoo wasps, quantitative studies on long-term population trends have not been carried out previously in this group. The probable main reasons are the difficulties of sampling large amounts of cuckoo wasps and that their identification always requires an experienced expert. Therefore, in contrast to some other insect groups with citizen science type of monitoring (Pöyry *et al*., 2009), documenting population trends of cuckoo wasps is only possible by examining existing museum and amateur collections of pinned individuals. Being difficult to identify can also be seen as an advantage in cuckoo wasps. This is because the pinned individuals in collections are likely to be much closer to a representative random sample from nature than pinned individuals of some easily identifiable insects in which museum collections may be heavily biased to rare species (see Kuussaari *et al*., 2007).

Assessing long-term population trends and distributional changes on the basis of natural history collections can also be difficult due to several other reasons, such as changes in sampling effort, changes in the spatial coverage of sampling and changes in collection methods over time (Jeppsson *et al*., 2010; Scheper *et al*., 2014). Numerous methods have been proposed in literature for taking these potential sources of bias into account in trend assessments (Isaac *et al*., 2014). The most commonly used methods employ data filtering or statistical correction procedures. Here, we employ the method of data filtering to examine population trends of cuckoo wasps.

Our study has four aims. First, we explore the general patterns of distribution and abundance of the cuckoo wasps recorded in Finland. Second, we investigate how the occurrence and distribution cuckoo wasps have changed during a period of 170 years. Based on observed changes in the occupancy of selected well-studied 10×10 km grid squares, we assess population trends for each species. Third, we analyse using comparative methods how species traits, specifically host specificity, body size, nesting type of host, abundance and size of distribution, are related to the observed trends. Fourth, we investigate how changes in the occurrence of specialist cuckoo wasps are correlated with changes in the occurrence of their hosts and test the prediction that changes in cuckoo wasps are more pronounced than changes in their hosts because they are positioned at a higher trophic level.

Materials and methods

Data collection

Distributional data of cuckoo wasps (Hymenoptera, Chrysididae) were collected primarily from private and

public Finnish entomological collections (Table 1). All the studied specimens were identified to species level by the author JPa using the key of Paukkunen *et al.* (2015). Additional data were obtained from ecological studies conducted by the Finnish Environment Institute (SYKE) and the Finnish Forest and Park Service (Metsähallitus) in 2004–2006. This material was also identified by the author JPa. Literature records were not included, except in a small number of cases concerning easily identifiable rare species. The final dataset included data on 18 584 specimens of cuckoo wasps collected within the current (i.e. post-WWII) borders of Finland in 1840–2015.

During the databasing process, georeferencing of specimens was performed using a 10 by 10 km grid of the Finnish coordinate reference system (YKJ or GRID27E). For specimens collected in 1972 (the establishment year of the YKJ system) or later, the coordinates of the collection locality were usually marked on the specimen label, but for older specimens, the coordinates were interpreted from the collection locality. If only the municipality name was mentioned in the label of the specimen or notebook of the collector, the coordinates were assessed according to the location of the central (church) village of the municipality. In old specimens, accurate information on the date of collection was often also missing from the label. In these cases, the year or at least decade of collection was estimated using notebooks of the collector and other available historical information.

In addition, data were collected of eight host species of cuckoo wasps. These species were selected to represent both cavity-nesting potter wasps [Vespidae, Eumeninae: *Ancistrocerus parietinus* (Linnaeus), *A. parietum* (Linnaeus), *Discoelius dufourii* Lepeletier, *Euodynerus notatus* (Jurine)] and ground-nesting digger wasps [Crabronidae: *Astata minor* (Kohl), *Cerceris arenaria* (Linnaeus), *C. quadrifasciata* (Panzer), *Philanthus triangulum* (Fabricius)]. All of them have at least one specialist or near specialist cuckoo wasp kleptoparasite species in Finland, enabling direct comparison of occurrence trends between the hosts and their natural enemies [*A. parietinus* – *Chrysis impressa* Schenck, *A. parietum* – *C. ignita* (Linnaeus), *D. dufourii* – *C. brevitarsis* Thomson and *C. equestris* Dahlbom, *E. notatus* – *C. graelsii* Guérin-Méneville and *C. pseudobrevitarsis* Linsenmaier, *A. minor* – *Hedychridium caputaureum* Trautmann & Trautmann, *C. arenaria* – *Hedychrum nobile* (Scopoli), *C. quadrifasciata* – *H. niemelai* Linsenmaier, *P. triangulum* – *H. rutilans* Dahlbom]. While some of the cuckoo wasps have also other host species, based on both published and unpublished evidence, we believe that the ones selected by us for comparison represent the most important host species in Finland. The host data were collected from the same sources as the cuckoo wasp data (Table 1), and nearly all specimens were identified by the author JPa. The host dataset consists of 4229 individuals, all collected within the current borders of Finland in 1840–2015.

The nomenclature follows Paukkunen *et al.* (2014) for cuckoo wasps and Fauna Europaea (Mitroiu, 2013) for the host species. The newly described species *Chrysis parietis* Budrys, 2016, which has been also recorded from Finland (Orlovskytė *et al.*, 2016), was omitted from our study due to its difficult identification, which requires DNA-barcoding. *Omalus aeneus* probably also consists of several closely related cryptic species in Finland (Paukkunen *et al.*, 2014), but these were not treated separately.

Table 1. Sources of cuckoo wasp data for the study.

Source	Number of specimens	%
Finnish Museum of Natural History (MZH)	11 544	62.1
Private collections (n = 28)	4903	26.4
Zoological Museum of the University of Turku	906	4.9
Zoological Museum of the University of Oulu	207	1.1
Other public collections (n = 6)*	231	1.2
Datasets of SYKE and Metsähallitus etc	775	4.2
Literature records	18	0.1
Total	18 584	100.0

*Department of Forest Sciences (University of Helsinki), Forssa Natural History Museum, Jyväskylä University Museum, Kuopio Natural History Museum, Lammi Biological Station, Natur-Museum Luzern.

Analysis of occurrence trends

In order to assess changes in the distribution areas of cuckoo wasps, the dataset was divided into two study periods so that the amount of data, as measured by the number of observed individuals, was as equal as possible in both periods. The first period covers the years 1840–1967 (9186 individuals) and the second period the years 1968–2015 (9398 individuals) (Table S1). The cut-off point of the study periods coincides relatively well with a major shift in land-use practices in Finland, including intensification of agriculture and forestry, as well as accelerating urbanisation (Luoto *et al.*, 2003). Dividing the data into three or more time periods with equal amounts of individuals would have resulted in undesirably unequal lengths of the periods, and therefore, we decided to reject analyses with more than two periods.

In the analyses of occurrence trends, we focused on changes in the occupancy of species in 10 × 10 km grid squares. Occupancy was calculated separately for both study periods, denoting the proportion of occupied squares (with at least one observed individual) to all studied squares of the period. Occurrence trends of each species were then assessed by measuring the relative change in occupancy between the two periods.

As a large proportion of all studied grid squares in both study periods included only sporadic records of a few individuals, we decided to focus on relatively well-

studied squares with at least 10 observed individuals per period, in order to assess temporal changes more reliably. These well-studied squares comprised less than half of the total number of squares in both periods, but approximately 90% of all individuals (Table S1). The first period included a total of 118 well-studied squares with 8547 individuals, while the second period included 155 well-studied squares with 8257 individuals.

The locations of the well-studied squares concentrated in southern Finland, which is also the area of highest cuckoo wasp species richness in the country. Both study periods included squares with agricultural areas, urban settlements and forested regions. On average, the squares of the second period located slightly more north-east than in the first period, but the difference was not statistically significant (Fig. 1, Table S1).

Statistical significance of the change in occupancy was analysed for each species using Fisher's exact test, and the resulting *P*-values were adjusted with a sequential Bonferroni correction (Rice, 1989). These statistical analyses were performed with the Statistix 9 software (Analytical Software, Tallahassee, FL, USA).

Species trait data

We included data on five species traits in the comparative analysis (see below): (i) abundance, (ii) size of distribution area, (iii) body length, (iv) host specificity and (v) nesting type of host (Table 2). The classification of each species is presented in Table S2.

Abundance was assessed according to the total number of individuals during both observation periods, while distribution size was measured as the total number of biogeographical provinces (Fig. 1) where the species has been observed. Body size was measured as the average of the minimum and maximum body lengths (mm) given for each species by Paukkunen *et al*. (2015).

Host specificity was presented as an ordinal variable with three categories, low, moderate and high, depending on the number and relatedness of host species in Finland. The categories were defined as follows: (i) low = species with two or more, distantly related (different tribes) host species; (ii) moderate = species with two or more, closely related (same tribe) host species; and (iii) high = species with apparently only one host species. Information of host species was extracted from Paukkunen *et al*. (2015) and other publications cited in it. Host species that do not occur in Finland were not taken into account, meaning that host specificity of a species was considered as high, if only one of its globally recorded host species had been recorded in Finland. Three species, *Chrysis westerlundi* Trautmann, *Elampus foveatus* (Mocsáry), *Holopyga inflammata* (Förster), whose hosts are completely unknown, were assigned to the category of moderate host specificity, as their closest relatives belonged to this category.

Finally, each cuckoo wasp species was classified into two categories according to the nesting type of its host species: (i) ground nesting (endogeic) or (ii) above ground/cavity nesting (epigeous). Nesting type is strongly correlated with habitat preference, as ground-nesting species typically live in sparsely vegetated open grasslands and cavity-nesting species prefer semi-open forest edges and gardens with dead wood.

Comparative analysis

We performed a comparative analysis between the occurrence changes (dependent variable) and species traits (explanatory/independent variables) to explore if the latter were connected with the observed population changes. Two rare species, *Chrysis corusca* Valkeila and *C. leptomandibularis* Niehuis, were omitted from the analysis due to their small numbers. Also *Hedychrum rutilans* was omitted, as it represented a strong outlier due to its exceptional increase.

To disentangle which combinations of explanatory variables show the most parsimonious fit to the data and to explore the overall relative importance of explanatory variables, we applied the approach of model selection (a.k.a. multi-model inference) (Burnham & Anderson, 2002). We fitted 30 generalised estimation equations (GEE) models including all possible combinations of the five explanatory variables while accounting for phylogenetic relatedness among cuckoo wasp species (discussed in the following section). The application of GEE models in comparative analysis was demonstrated by Paradis and Claude (2002). The fitted models were ranked according to their information criterion value (here quasi-likelihood information criterion, QIC; Pan, 2001) from the smallest to the highest (i.e. from the most to the least parsimonious model). For each model, we calculated the 'QIC weight' that represents the likelihood that a model shows the best fit to the data (Johnson & Omland, 2004). Following this, the relative importance of each explanatory term was calculated by summing QIC weights across those models where the respective term was present.

To account for potentially confounding effects of phylogenetic relatedness among the study species, we derived a phylogenetic hypothesis for the included 45 focal species (Appendix S1). We included this information in the analyses by calculating a species-to-species correlation matrix and by fitting generalised estimation equations (GEE) as implemented in the APE library ('compar.gee' function command), version 3.3 (Paradis, 2006) within the R statistical environment, version 3.2.2 (R Core Team, 2015). We used a 'Gaussian' error structure and identity link functions in all models.

Comparison of cuckoo wasps and their hosts

Occurrence trends of the selected eight host species were analysed similarly to the cuckoo wasps. The first period included a total of 67 well-studied squares with at least 10

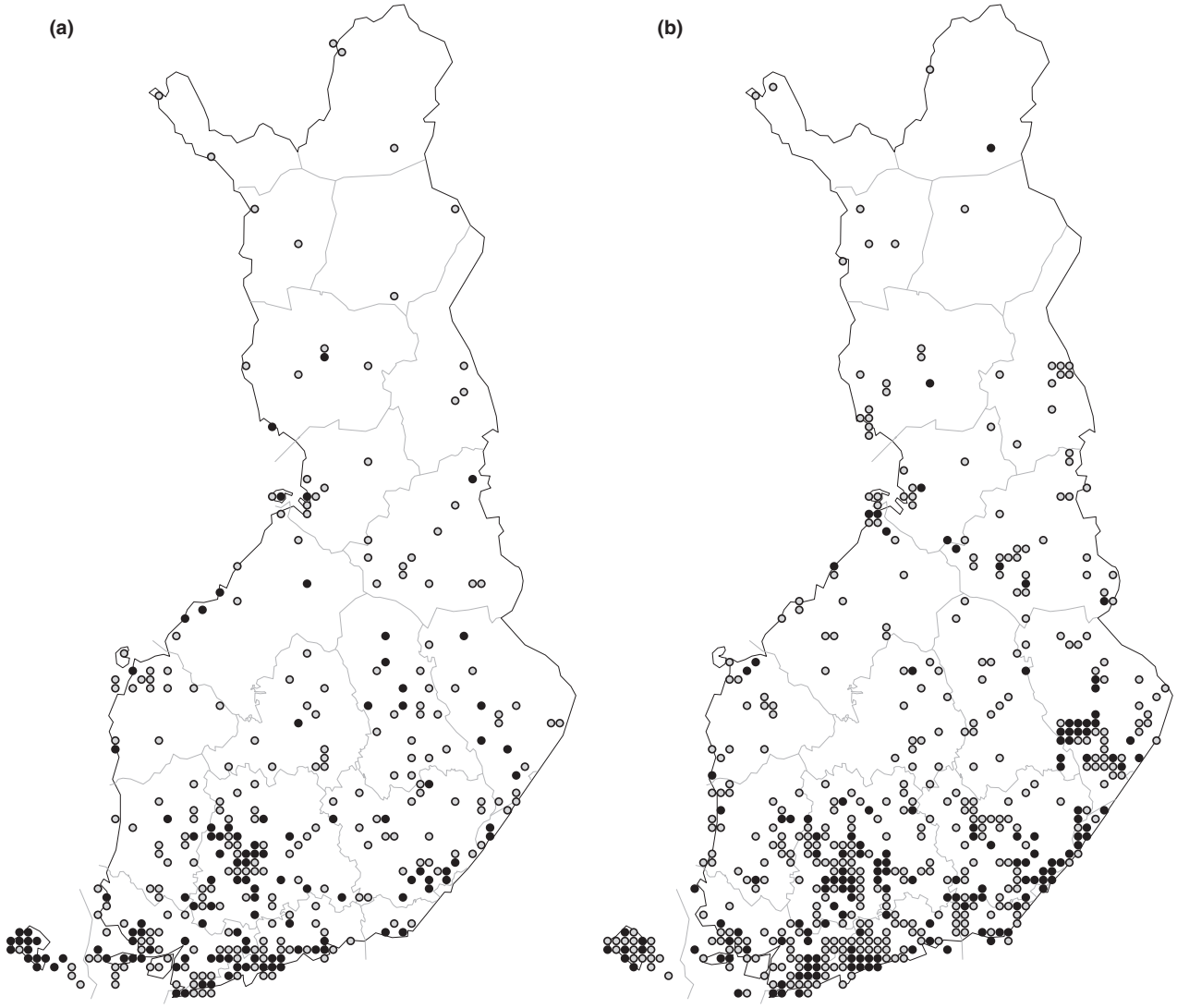

Fig. 1. Locations of cuckoo wasp records during the two study periods (a) 1840–1967 and (b) 1968–2015 in Finland. Well-studied 10 × 10 km grid squares, with at least ten individuals, are shown by black dots. Other squares are shown by grey dots. Thin grey lines indicate the borders of biogeographical provinces.

host individuals, while the second period included a total of 40 well-studied squares (Table S1). The total number of individuals, as well as the average number of individuals per square, was approximately two times higher during the first than the second study period. This means that the average occurrence level of stable species would have been higher during the first than the second study period just because of the much larger number of recorded individuals (i.e. larger study effort) during the first study period. Therefore, we decided to even out the number of individuals of the study periods by random sampling. This was done by randomly removing records from the first study period until the total number of individuals corresponded with the second period, while forcing at least one record from each 67 well-studied square to stay in the dataset. The sampled dataset was then used for assessing changes in the occupancy of the species. The dependence between the occurrence trends of the hosts and their specialist cuckoo wasp kleptoparasites (10 species) was studied using Spearman's correlation analysis. We also tested whether changes in occurrence were larger in cuckoo wasps than in their hosts by using Wilcoxon's signed-rank test.

Results

The results showed a relatively steady increase in cuckoo wasp records from the 1840s to 2010s, except in the 1980s and 1990s when collecting activity was temporarily lower

Table 2. An overview of the cuckoo wasp species traits included in the comparative analysis of the 48 cuckoo wasp species.

Species trait	Description (and the observed range in the data)	Type
Abundance	Total number of individuals recorded (1–3082)	Continuous
Distribution size	Number of Finnish biogeographical provinces in which the species has been recorded (1–20)	Continuous
Body size	Average body length (mm) (3.0–11.5)	Continuous
Host specificity	1 = low (n = 9), 2 = moderate (n = 27), 3 = high (n = 12), depending on the number and relatedness of host species	Ordinal
Nesting type of host	1 = not nest building (n = 2), 2 = ground-nesting (n = 21), 3 = above ground-nesting (n = 25)	Categorical

(Fig. S2). The cumulative species number has not risen markedly after the 1950s, which indicates that the Finnish fauna is well-known and new species are hard to find. A more detailed summary on temporal variation in study effort is presented in Appendix S2.

Relative abundance and commonness of species

The frequency distribution of Finnish cuckoo wasps turned out to be strongly skewed, with only a few very common species and many rare species (Fig. 2). The most abundant species was *Chrysis angustula* Schenck, which comprised 17% of all recorded individuals, while the next most abundant species, *Hedychrum nobile*, constituted 8% of all individuals. The relative abundance of 20 species was <1%. Commonness, as measured by the number of 10 × 10 km squares, was strongly correlated with abundance (Spearman's correlation coefficient 0.94, $P < 0.001$).

Occurrence trends of individual species

The relative change in occupancy of 10 × 10 km squares was negative for 38 cuckoo wasp species and positive for eight species, when only the well-studied squares were taken into account (average change −10%) (Table 3A). When all squares were included, the change was negative for 39 species and positive for eight species (average change −15%). According to Fisher's exact test, the change in occupancy in the well-studied squares was statistically significant for 20 species and nearly significant for an additional five species. After Bonferroni correction of the P-values, the change in occupancy remained significant for 11 species: *Chrysis graelsii* (relative change in occupancy −84%), *Pseudospinolia neglecta* Shuckard (−82%), *Chrysis iris* Christ (−76%), *Chrysis ignita* (−72%), *Chrysis ruddii* Shuckard (−70%), *Chrysis borealis* Paukkunen *et al.* (−65%), *Chrysis longula* Abeille de Perrin (−59%), *Chrysis pseudobrevitarsis* (−56%), *Pseudomalus auratus* (Linnaeus) (−48%), *Chrysis solida* Haupt (−47%) and *Trichrysis cyanea* (Linnaeus) (−39%). In all these species, the occurrence trend was thus decreasing.

In the selected eight host species, occurrence changes were positive for six species and negative for two species, when only the well-studied squares were included (Table 3B). According to Fisher's exact test, the change in the well-studied squares was statistically significant in three species and nearly significant in one additional species. After Bonferroni correction of the P-values, only one host species, *Euodynerus notatus*, had a significant change in occupancy (−53%).

Comparative species trait data analysis

According to the model selection analysis of the occurrence trends, one of the 30 fitted GEE models was outstandingly likely (P = 1.000) the best (i.e. most parsimonious) model, including three explanatory variables, abundance (variable coefficient = 0.013), body size (coeff. = 5.614) and nesting type (coeff. = −29.743). The results indicate that scarce and small species that use above ground-nesting hosts declined more than abundant and large species that use ground-nesting hosts (Table S3).

Comparison of cuckoo wasps and their hosts

The occurrence trends of cuckoo wasps and their hosts were significantly positively correlated (Table 4, Fig. 3). Spearman's correlation coefficient between the eight host species and ten more or less specialised cuckoo wasp species was 0.726 (P = 0.021). If the strongly increasing species *Hedychrum rutilans* and its host *Philanthus triangulum* were removed from the analysis, the correlation coefficient remained marginally significant, 0.622 (P = 0.076). The changes in occurrence were generally larger in cuckoo wasps than in their hosts. In seven of the eight species pairs, in which the observed trend was in the same direction, the change was larger in cuckoo wasps (P-value of Wilcoxon signed-rank test 0.05).

Hedychrum rutilans, which is a specialist kleptoparasite of the bee wolf, *Philanthus triangulum* (Crabronidae), has increased drastically during the last decades (Fig. 3a, b), although the change was not statistically significant due to

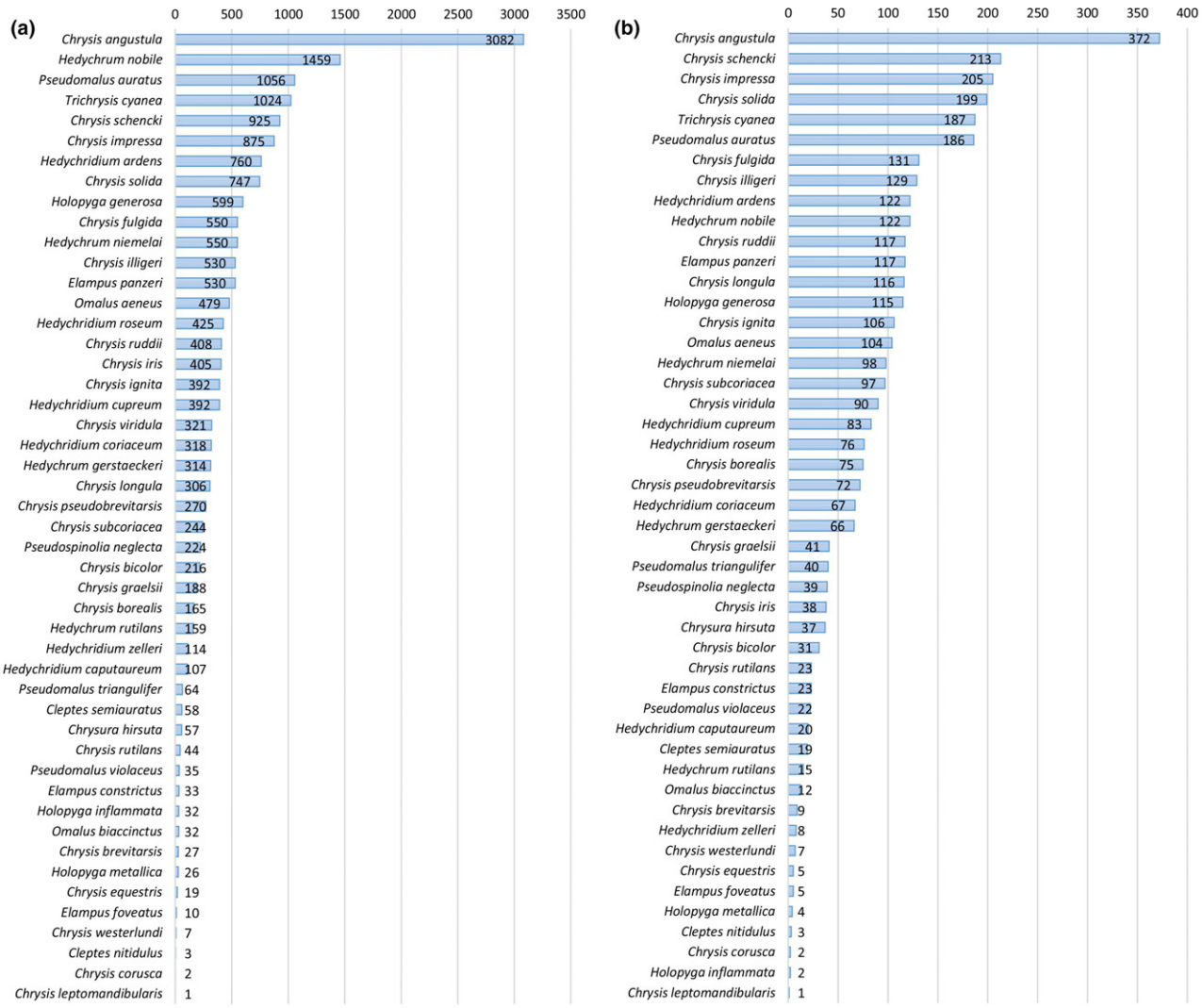

Fig. 2. (a) Relative abundance (total number of individuals) and (b) commonness (total number of 10 × 10 km squares) of Finnish cuckoo wasps based on the study material. [Colour figure can be viewed at wileyonlinelibrary.com]

the relatively low total number of records. According to our data, the host increased its occupancy by 235%, while the kleptoparasite increased by 813% between the two observation periods. *Chrysis graelsii*, however, is an example of a cuckoo wasp species, which has undergone a serious decline in Finland during the 20th century (Fig. 3c, d). Its main host in Finland is the solitary wasp *Euodynerus notatus*, which nests in dead wood, especially in the walls of sun-exposed old log buildings. To a minor extent, also *E. quadrifasciatus*, can serve as its host. The occupancy of *C. graelsii* decreased by 84% between the two study periods, while the occupancy of *E. notatus* decreased by 53%.

Discussion

We have presented here a quantitative analysis of population changes within a little studied insect group, cuckoo wasps. In general, there is a lack of comprehensive and quantitative overviews of insect groups with parasitoid or kleptoparasitic life cycles (Hochberg, 2000; Shaw & Hochberg, 2001). Studies on the occurrence changes of insects have largely focused on more popular species groups, such as butterflies, moths, beetles and dragonflies in Europe (e.g. Warren *et al.*, 2001; Conrad *et al.*, 2004; Groenendijk & van der Meulen, 2004; Thomas, 2005; Kuussaari *et al.*, 2007; Jeppsson *et al.*, 2010; Angert *et al.*, 2011; Fox *et al.*, 2014; Powney *et al.*, 2015). The order Hymenoptera has received relatively little attention in this respect, although population trends of bees, and especially bumblebees, have been studied more extensively (e.g. Biesmeijer *et al.*, 2006; Kosior *et al.*, 2007; Potts *et al.*, 2010; Scheper *et al.*, 2014).

Of the 48 studied Finnish cuckoo wasp species, a total of 11 species (23%) had declined significantly between the

Table 3. Changes in the occupancy of grid squares across (a) cuckoo wasps and (b) selected eight host species between the two study periods (1840–1967 and 1968–2015). The change is measured as the relative difference in occupancy between the two study periods.

A. Cuckoo wasp species	Occupancy (%) in selected well-studied squares (n = 232)		Relative change in occupancy (%)	P-value of Fisher's exact test	Average trend in all squares (n = 700)
	1840–1967	1968–2015			
Chrysis angustula	79.7	77.4	−2.8	0.660	−0.5
Chrysis bicolor	16.1	8.4	−47.9	0.058	−45.6
Chrysis borealis	28.0	9.7	−65.4	<0.001*	−63.1
Chrysis brevitarsis	2.5	3.9	52.3	0.736	28.0
Chrysis corusca	0.0	1.3		0.507	
Chrysis equestris	2.5	1.3	−49.2	0.655	−57.3
Chrysis fulgida	44.9	34.2	−23.9	0.080	−28.6
Chrysis graelsii	24.6	3.9	−84.2	<0.001*	−86.8
Chrysis ignita	50.0	14.2	−71.6	<0.001*	−75.4
Chrysis illigeri	44.9	40.6	−9.5	0.537	−10.2
Chrysis impressa	49.2	60.0	22.1	0.086	42.0
Chrysis iris	24.6	5.8	−76.4	<0.001*	−83.1
Chrysis leptomandibularis	0.0	0.0			−100.0
Chrysis longula	53.4	21.9	−58.9	<0.001*	−62.9
Chrysis pseudobrevitarsis	36.4	16.1	−55.7	<0.001*	−56.0
Chrysis ruddii	54.2	16.1	−70.3	<0.001*	−68.4
Chrysis rutilans	11.0	5.2	−53.2	0.107	−54.3
Chrysis schencki	61.0	53.5	−12.2	0.221	−1.3
Chrysis solida	72.0	38.1	−47.2	<0.001*	−54.1
Chrysis subcoriacea	36.4	31.6	−13.2	0.439	−17.3
Chrysis westerlundi	1.7	2.6	52.3	0.701	60.0
Chrysis viridula	33.1	22.6	−31.7	0.056	−32.1
Chrysura hirsuta	12.7	7.1	−44.2	0.146	−53.5
Cleptes nitidulus	1.7	0.6	−61.9	0.580	−68.0
Cleptes semiauratus	4.2	7.7	82.7	0.314	4.0
Elampus constrictus	5.1	3.9	−23.9	0.768	−0.5
Elampus foveatus	2.5	1.9	−23.9	1.000	−36.0
Elampus panzeri	33.1	23.9	−27.8	0.103	−18.0
Hedychridium ardens	46.6	27.7	−40.5	0.001	−44.8
Hedychridium caputaureum	6.8	6.5	−4.8	1.000	−21.8
Hedychridium coriaceum	28.8	16.8	−41.8	0.019	−43.8
Hedychridium cupreum	37.3	20.0	−46.4	0.002	−43.5
Hedychridium roseum	26.3	21.9	−16.5	0.474	−18.2
Hedychridium zelleri	2.5	1.9	−23.9	1.000	−48.8
Hedychrum gerstaeckeri	11.9	27.7	133.8	0.002	120.0
Hedychrum niemelai	20.3	38.1	87.2	0.002	54.8
Hedychrum nobile	29.7	39.4	32.7	0.125	42.9
Hedychrum rutilans	0.8	7.7	813.5	0.008	795.9
Holopyga generosa	38.1	30.3	−20.5	0.197	−6.4
Holopyga inflammata	1.7	0.0	−100.0	0.186	−100.0
Holopyga metallica	2.5	0.6	−74.6	0.318	−57.3
Omalus aeneus	33.9	21.9	−35.3	0.029	−39.3
Omalus biaccinctus	9.3	1.9	−79.2	0.010	−82.5
Pseudomalus auratus	71.2	36.8	−48.3	<0.001*	−57.5
Pseudomalus triangulifer	15.3	8.4	−45.0	0.085	−36.0
Pseudomalus violaceus	10.2	1.9	−81.0	0.004	−46.7
Pseudospinolia neglecta	25.4	4.5	−82.2	<0.001*	−84.0
Trichrysis cyanea	71.2	43.2	−39.3	<0.001*	−42.2

B. Host species	Occupancy (%) in selected well-studied squares (n = 95)		Relative change in occupancy (%)	P-value of Fisher's exact test[1]	Average trend in all squares (n = 396)
	1840–1967	1968–2015			
Ancistrocerus parietinus	70.1	72.5	3.4	0.795	−12.3
Ancistrocerus parietum	50.7	32.5	−36.0	0.066	−63.0
Astata minor	9.0	15.0	67.5	0.338	−18.9
Cerceris arenaria	43.3	75.0	73.3	0.001	18.7
Cerceris quadrifasciata	44.8	50.0	11.7	0.600	−18.7
Discoelius dufourii	14.9	22.5	50.8	0.321	−25.2
Euodynerus notatus	79.1	37.5	−52.6	<0.001*	−59.9
Philanthus triangulum	10.4	35.0	235.0	0.002	295.5

*Trend significant after Bonferroni correction.

two studied time periods, whereas none had increased significantly (although the increase of *Hedychrum rutilans* was nearly significant). In addition, two species that were not recorded during the latter time period (*Chrysis leptomandibularis* and *Holopyga inflammata*) may already have gone extinct in Finland. The proportion of declining species versus increasing species is unusually high in the Finnish cuckoo wasps compared with other studied insect groups, even in a global perspective. For example, in a long-term study on Finnish butterflies, the proportion of declining species was estimated to be 31%, while 36% of species were considered as increasing (Kuussaari *et al*., 2007). In Swedish long-horn beetles, 40% of species were regarded as declining and 60% as increasing (Jeppsson *et al*., 2010). In Great Britain, however, the percentage of decreasing moth species was found to be much higher than that of increasing species (Conrad *et al*., 2004; Fox *et al*., 2014). The large proportion of declining species in cuckoo wasps has earlier been anticipated in the national Red List assessment (Paukkunen, 2010).

Population trends and species traits

According to our comparative analysis, changes in the occurrence were associated with abundance and body size of cuckoo wasps and nesting type of the host species. Abundant species declined less than scarce species, which might be due to their less demanding environmental requirements and thus stronger resilience to environmental changes (Warren *et al*., 2001). Abundance was positively correlated with range size, indicating that widespread species generally also declined less than narrow-ranged species. However, distribution size did not enter the best model in the comparative analysis. The lower occurrence trends of rare and narrow-ranged species could be a sign of biotic homogenisation, where abundant and widespread species gradually replace other taxa (Warren *et al*., 2001; Ekroos *et al*., 2010; Powney *et al*., 2015).

Body size was positively associated with occurrence trend, indicating that small species generally declined more than large species. Previous studies of Hymenoptera have shown that small body size may correlate with poor dispersal ability and therefore cause vulnerability to environmental changes, such as habitat fragmentation (Gathmann *et al*., 1994; Gathmann & Tscharntke, 2002; Greenleaf *et al*., 2007; Bommarco *et al*., 2010). Small body size is also linked to high temporal fluctuations in population size (Henle *et al*., 2004), which may further increase sensitivity to habitat loss. Other studies, however, have reported opposing or unclear effects of body size. For example, Bartomeus *et al*. (2013) and Scheper *et al*. (2014) found a negative correlation between body size and occurrence trend in bees, while Williams *et al*. (2010) did not find any clear overall effect.

Cuckoo wasps that have hosts nesting above ground (cavity nesters) had more negative occurrence trends than those with ground-nesting hosts (ground nesters). This could be caused by more severe changes in the habitats of cavity nesters or by higher sensitivity to environmental changes in cavity nesters compared to ground nesters. It is obvious that both groups have suffered from habitat loss and degradation in Northern Europe during the last century. While the decrease of sun-exposed dead wood in forests and agricultural landscapes has been detrimental for cavity nesters, overgrowth of open sparsely vegetated habitats, such as dry meadows and sands, has been harmful for ground nesters. Road verges, sand pits and ruderal areas have probably offered new habitats for ground nesters and partly compensated for the loss of original habitats, whereas cavity nesters have not been able to find suitable habitats from intensively managed forests or modern agricultural areas. Especially, the loss of traditional wooden constructions, such as log barns and houses, has had adverse effects on cavity nesters (Szczepko *et al*., 2013).

A higher vulnerability of cavity-nesting compared with ground-nesting hymenopterans has also been observed in earlier studies. Williams *et al*. (2010) observed that bee species nesting above ground were on average more negatively affected by isolation and agricultural intensification (excluding tillage) than were species nesting in the ground. The result was explained by the more flexible habitat requirements of ground nesters, which can find suitable

Table 4. Comparison of the occurrence trends of cuckoo wasps and their hosts (statistically significant changes in bold).

Cuckoo wasp	Relative change in occupancy (%)	*P*-value of Fisher's exact test	Host	Relative change in occupancy (%)	*P*-value of Fisher's exact test
Chrysis graelsii	**−84.2**	<0.001	*Euodynerus notatus*	**−52.6**	<0.001
Chrysis ignita	**−71.6**	<0.001	*Ancistrocerus parietum*	−36.0	0.066
Chrysis pseudobrevitarsis	**−55.7**	<0.001	*Euodynerus notatus*	**−52.6**	<0.001
Chrysis equestris	−49.2	0.655	*Discoelius dufourii*	50.8	0.321
Hedychridium caputaureum	−4.8	1.000	*Astata minor*	67.5	0.338
Chrysis impressa	22.1	0.086	*Ancistrocerus parietinus*	3.4	0.795
Hedychrum nobile	32.7	0.125	*Cerceris arenaria*	**73.3**	0.001
Chrysis brevitarsis	52.3	0.736	*Discoelius dufourii*	50.8	0.321
Hedychrum niemelai	**87.2**	0.002	*Cerceris quadrifasciata*	11.7	0.600
Hedychrum rutilans	**813.5**	0.008	*Philanthus triangulum*	**235.0**	0.002

nesting sites, for example, from field verges. Steffan-Dewenter *et al.* (2006) reported that the proportion of cavity-nesting versus ground-nesting bees was positively correlated with habitat area in lime-stone quarries, indicating an increased sensitivity to habitat size in cavity nesters. The authors concluded that nesting sites of cavity nesters seem to be a limiting factor in most habitats, and therefore, cavity nesters have lower densities and are more prone to extinction.

The two variables, which were not selected in the best model of the comparative analysis, were host specificity and size of distribution area. Previous studies have shown that food/nutritional specialists are often more vulnerable to environmental changes than generalists (e.g. Kotiaho *et al.*, 2005; Bommarco *et al.*, 2010; Öckinger *et al.*, 2010; Bartomeus *et al.*, 2013), and therefore, we also expected to find a negative dependence between occurrence trends and host specificity. The lack of this dependence could be caused by the fact that specialised cuckoo wasps tend to have common host species that probably have retained stable populations during the study time. The host species of cuckoo wasps are still relatively poorly known, and therefore, our classification of host specificity should only be considered tentative. A study on British butterflies indicated that the relationship between population trends and niche breadth can also be non-linear, as moderately generalist species were found to be more sensitive than specialists or extreme generalists (Dapporto & Dennis, 2013).

According to our analysis, distribution size did not seem to have an influence on occurrence trends. However, as mentioned earlier, distribution size and abundance were positively correlated, and therefore, only one of these variables could enter the best model as an explanatory term. The positive inter-specific relationship between abundance and distribution is a general macroecological pattern that has been observed in numerous studies (Hanski *et al.*, 1993).

Comparing trends of cuckoo wasps and their hosts

Changes in occurrence were generally larger in cuckoo wasps than in their hosts, although the difference was only marginally statistically significant due to the small number of studied host species. This result is in accordance with our expectations, as species at higher trophic ranks are predicted to be more sensitive to environmental changes than species at lower ranks (Hawkins, 1994; Holt, 1996). For example, Komonen *et al.* (2000) found that habitat loss and fragmentation in boreal forests truncated food chains of specialised species in the course of time since isolation, and parasitoid wasps were more affected than their hosts. Moreover, Roslin *et al.* (2013) studied plant and insect communities on islands of various sizes and showed that food chain length decreased from large to small islands. Parasitoid wasps were thus more sensitive to island size variation than organisms at lower trophic levels. In their study on insect communities of *Vicia sepium*, Kruess and Tscharntke (2000) observed that parasitoids suffered more from habitat loss and isolation than their phytophagous hosts, and parasitoids were also more sensitive to habitat patch size. While increased sensitivity means larger declines in parasitoid species compared with their hosts, it could also denote larger increases in parasitoids, when the host species are increasing. This seems to be the case in *Hedychrum rutilans* and its host *Philanthus triangulum*, as the cuckoo wasp has gone through a significantly larger relative increase compared with its host between the two study periods.

Data evaluation

A possible source of bias in our dataset could have been caused by changes in sampling methods during the study time. Traditionally cuckoo wasps have been collected by nets, but in recent decades, different types of traps have gained popularity. Especially yellow pan traps have become popular in entomological surveys. It is probable that ground-nesting wasps are more attracted to pan traps than cavity-nesting wasps, as the traps are usually placed on sparsely vegetated spots on the ground. Consequently, the proportion of ground-nesting species could be over-represented in recently collected material

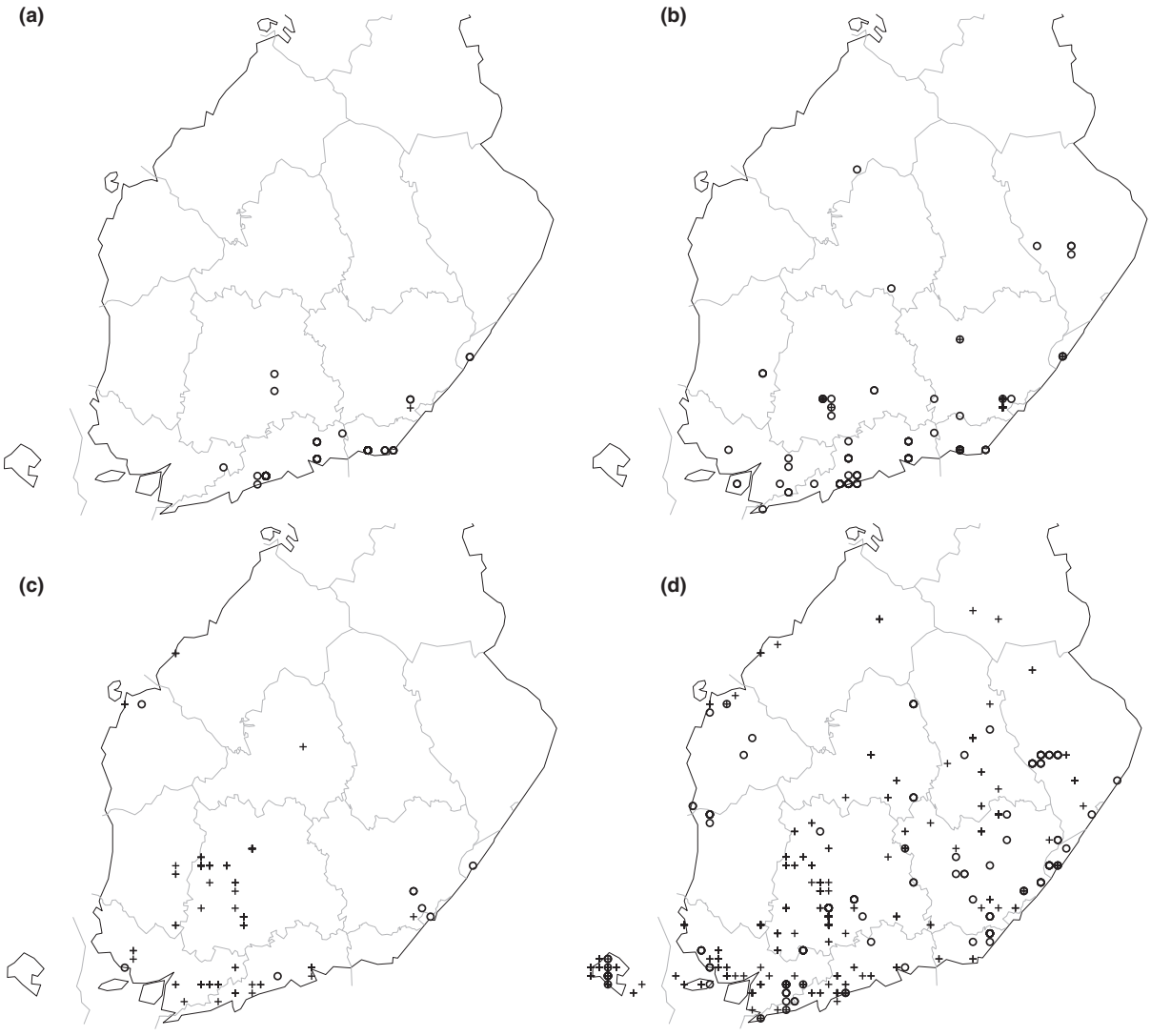

Fig. 3. Distributional changes of cuckoo wasps and their hosts in southern Finland. Increasing species: (a) *Hedychrum rutilans* and (b) *Philanthus triangulum* (host). Declining species: (c) *Chrysis graelsii* and (d) *Euodynerus notatus* (host). [+] = recorded in 1840–1967, [○] = recorded in 1968–2015, [⊕] = recorded in both 1840–1967 and 1968–2015. Borders of biogeographical provinces are shown with thin lines.

compared to older collections. This bias is, however, difficult to take into account, as the collection method is usually not known for older collected specimens. Eliminating all trapped specimens would also have decreased the size of the dataset substantially.

Another potential source of bias is caused by changes in the accuracy of reporting collection localities. The national coordinate system (YKJ or GRID27E) was introduced in the beginning of the 1970s, and before this, only locality names were used for reporting collection localities for Finnish entomological specimens. Usually merely the name of the municipality was mentioned, which might have led to an artificial aggregation of old records into certain 10×10 km squares in our dataset, as georeferencing was done according to the central church villages. The problem of spatial aggregation of records during the first observation period could have been somewhat mitigated by applying a larger grid, for example, of 50×50 km squares. This, however, would have caused a loss in resolution and lowered the number of significant trend estimates. A sufficiently fine-scaled grid is essential for a reliable assessment of rarity, trends and extinction risk of species (Hartley & Kunin, 2003; Wilson *et al.*, 2004).

Difficulties in trend assessments based on natural history collections can depend on the studied taxa. For example, biases caused by changes in collection methods and changes of charisma of species are potentially more

important for popular and attractive groups, such as butterflies and moths and beetles, than for less studied groups (Jeppsson *et al*., 2010). In cuckoo wasps, most species are rather similar in general appearance and species identification is often difficult or impossible without a microscope. Therefore, they are collected more randomly than are specimens of other insect groups with great specific differences in external morphology. Although some cuckoo wasps species are detected more readily than others in nature, proportions of specimens in collections probably reflect actual abundances more reliably than in, e.g., butterflies that are skewed towards rare species (Kuussaari *et al*., 2007).

Changes in the occurrence of cuckoo wasps were assessed here by comparing relative occupancies in two study periods with approximately equal amounts of records. As there were only two long study periods (length 128 and 48 years, respectively) which were compared, the observed changes in occurrence represent a rough estimate of long-term population trends. Most species are likely to have substantial fluctuations in their population sizes during shorter time-scales, such as decades and single years, which unfortunately remain unnoticed in our study. However, in spite of these shortcomings, our study setting produces valuable and novel information on long-term trends in a poorly known insect group. This is particularly important, as in rare species, detailed analyses of population trends are typically overly difficult due to the poor availability of data.

Conclusions

Our results indicate that cuckoo wasps have suffered from environmental changes more than most other insect groups, as the proportion of declining species is exceptionally high. Undoubtedly, habitat loss and degradation has had a negative influence on cuckoo wasps, because changes in agriculture and forestry have dramatically diminished the amount of suitable nesting sites of their hosts, such as forest margins with sun-exposed dead wood and dry meadows with sparse vegetation. The kleptoparasitic and parasitoid lifestyle and high trophic position of cuckoo wasps have further increased their susceptibility to environmental changes. Species with hosts nesting above ground, that are dependent on dead wood, were found to have more negative trends than those with ground-nesting hosts, probably because ground nesters are able to utilise road verges, sand pits and ruderal areas as novel secondary habitats. The severe decline of cuckoo wasps with hosts nesting above ground underlines the importance of preserving sun-exposed dead wood in forests and old wooden constructions in agricultural and urban areas.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12241:

Appendix S1. Details of building the phylogenetic hypothesis.

Appendix S2. General trends in Finnish cuckoo wasps

Table S1. Summary of the data used in the analyses of occurrence trends of (a) cuckoo wasps and (b) their hosts.

Table S2. Species traits and red list categories of Finnish cuckoo wasps.

Table S3. Results of model selection (a.k.a. multi-model inference) analysis for the occurrence trends (1968–2014 vs. 1840–1967) of cuckoo wasps as the response variable, with different combinations of abundance, body size, distribution size, host specificity and nesting type of host (model coefficients are given for terms included in a model).

References

Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J. (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, **14**, 677–689.

Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M. & Winfree, R. (2013) Historical changes in northeastern US bee pollinators related to shared ecological traits. *PNAS*, **110**, 4656–4660.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I. & Öckinger, E.O. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B*, **277**, 2075–2082.

Burnham, K.B. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York City, New York.

Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R. & Warren, M.S. (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation*, **8**, 119–136.

Cousins, S.A.O., Auffret, A.G., Lindgren, J. & Tränk, L. (2015) Regional-scale land-cover change during the 20th century and its consequences for biodiversity. *Ambio*, **44**, 17–27.

Dapporto, L. & Dennis, R.L.H. (2013) The generalist-specialist continuum: testing predictions for distribution and trends in British butterflies. *Biological Conservation*, **157**, 229–236.

Ekroos, J., Heliölä, J. & Kuussaari, M. (2010) Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology*, **47**, 459–467.

Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D. & Roy, D.B. (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology*, **51**, 949–957.

Gathmann, A., Greiler, H.J. & Tscharntke, T. (1994) Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. *Oecologia*, **98**, 8–14.

Gathmann, A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology*, **71**, 757–764.

Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**, 589–596.

Groenendijk, D. & van der Meulen, J. (2004) Conservation of moths in The Netherlands: population trends, distribution patterns and monitoring techniques of day-flying moths. *Journal of Insect Conservation*, **8**, 109–118.

Gunton, R.M. & Pöyry, J. (2016) Scale-specific spatial density-dependence in parasitoids: a multi-factor meta-analysis. *Functional Ecology*, **30**, 1501–1510.

Hanski, I., Kouki, J. & Halkka, A. (1993) Three explanations of the positive relationship between distribution and abundance of species. *Species Diversity in Ecological Communities*, pp. 108–116. (ed. by R.E. Ricklefs and D. Schluter), The University of Chicago Press, Chicago, Illinois.

Hartley, S. & Kunin, W.E. (2003) Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology*, **17**, 1559–1570.

Hawkins, B.A. (1994) *Pattern and Process in Host-Parasitoid Interactions*. Cambridge University Press, Cambridge, UK.

Henle, K., Davies, K.F., Kleyer, M., Margules, C.R. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207–251.

Hochberg, M.E. (2000) What conserve parasitoids?. *Parasitoid Population Biology*, pp. 266–277. (ed. by M.E. Hochberg and A.R. Ives), Princeton University Press, Princeton, New Jersey.

Holt, R.D. (1996) Food webs in space: an island biogeographical perspective. *Food Webs*, pp. 313–323. (ed. by G.A. Polis and K.O. Winemiller), Chapman Hall, New York City, New York.

Hyvärinen, E., Kouki, J. & Martikainen, P. (2006) Fire and green-tree retention in conservation of red-listed and rare deadwood dependent beetles in boreal borests. *Conservation Biology*, **20**, 1711–1719.

Isaac, N.J.B., Van Strien, A.J., August, T.A., De Zeeuw, M.P. & Roy, D.B. (2014) Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, **5**, 1052–1060.

Iyengar, E.V. (2008) Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. *Biological Journal of the Linnean Society*, **93**, 745–762.

Jeppsson, T., Lindhe, A., Gärdenfors, U. & Forslund, P. (2010) The use of historical collections to estimate population trends: a case study using Swedish longhorn beetles (Coleoptera: Cerambycidae). *Biological conservation*, **143**, 1940–1950.

Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.

Kimsey, L.S. & Bohart, R.M. (1991) *[1990] The Chrysidid Wasps of the World*. Oxford Press, New York City, New York.

Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. (2000) Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos*, **90**, 119–126.

Kosior, A., Celary, W., Olejniczak, P., Fijał, J., Król, W., Solarz, W. & Płonka, P. (2007) The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of western and central Europe. *Oryx*, **41**, 79–88.

Kotiaho, J.S., Kaitala, V., Komonen, A. & Päivinen, J. (2005) Predicting the risk of extinction from shared ecological characteristics. *PNAS*, **102**, 1963–1967.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. (2001) Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scandinavian Journal of Forest Research*, **16**, 27–37.

Kruess, A. & Tscharntke, T. (2000) Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia*, **122**, 129–137.

Kuussaari, M., Heliölä, J., Pöyry, J. & Saarinen, K. (2007) Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. *Journal of Insect Conservation*, **11**, 351–366.

Larsson, A. (2015) Rödlista över steklar Hymenoptera. *Rödlistade arter i Sverige 2015* (ed. by ArtDatabanken), pp. 92–97. ArtDatabanken SLU, Uppsala, Sweden.

Luoto, M., Rekolainen, S., Aakkula, J. & Pykälä, J. (2003) Loss of plant species richness and habitat connectivity in grasslands associated with agricultural change in Finland. *Ambio*, **32**, 447–452.

Mitroiu, M.-D. (2013) *Fauna Europaea: Hymenoptera, Apocrita*. Fauna Europaea version 2.6. <http://www.fauna-eu.org>

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S. & Bommarco, R. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology letters*, **13**, 969–979.

Ødegaard, F., Lønnve, O. & Hanssen, L.O. (2015) Vepser. Hymenoptera. *Norsk rødliste for arter 2015* (ed. by S. Henriksen and O. Hilmo), pp. 173–180. Artsdatabanken, Trondheim, Norway.

O'Neill, K.M. (2001) *Solitary Wasps: Behavior and Natural History*. Cornell University Press, Ithaca, New York.

Orlovskytė, S., Budrys, E., Budrienė, A., Radzevičiūtė, R. & Soon, V. (2016) Sibling species in the *Chrysis ignita* complex: molecular, morphological and trophic differentiation of Baltic species, with a description of two new cryptic species (Hymenoptera: Chrysididae). *Systematic Entomology*, **41**, 771–793.

Paillet, Y., Bergès, L., Hjältén, J., Òdor, P., Avon, C., Bernhardt-Romermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Meszaros, I., Sebastia, M.T., Schmidt, W., Standovar, T., Tothmeresz, B., Uotila, A., Valladares, F., Vellak, K. & Virtanen, R. (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conservation Biology*, **24**, 101–112.

Pan, W. (2001) Akaike's information criterion in generalized estimating equations. *Biometrics*, **57**, 120–125.

Paradis, E. (2006) *Analysis of Phylogenetics and Evolution With R*. Springer, New York City, New York.

Paradis, E. & Claude, J. (2002) Analysis of comparative data using generalized estimation equations. *Journal of Theoretical Biology*, **218**, 175–185.

Pärn, M., Soon, V., Vallisoo, T., Hovi, K. & Luig, J. (2014) Host specificity of the tribe Chrysidini (Hymenoptera, Chrysididae) in Estonia ascertained with trap-nesting. *European Journal of Entomology*, **112**, 91–99.

Paukkunen, J. (2010) Stinging wasps. *The 2010 Red List of Finnish Species*, pp. 529–544. (ed. by P. Rassi, E. Hyvärinen, A. Juslén and I. Mannerkoski), Finnish Ministry of Environment and Finnish Environment Institute, Helsinki, Finland.

Paukkunen, J., Berg, A., Soon, V., Ødegaard, F. & Rosa, P. (2015) An illustrated key to the cuckoo wasps (Hymenoptera. Chrysididae) of the Nordic and Baltic countries, with description of a new species. *ZooKeys*, **548**, 1–116.

Paukkunen, J., Rosa, P., Soon, V., Johansson, N. & Ødegaard, F. (2014) Faunistic review of the cuckoo wasps of Fennoscandia, Denmark and the Baltic countries (Hymenoptera: Chrysididae). *Zootaxa*, **3864**, 1–67.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, **25**, 345–353.

Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'Eman, G. & Willmer, P. (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, **30**, 78–85.

Powney, G.D., Cham, S.S.A., Smallshire, D. & Isaac, N.J.B. (2015) Trait correlates of distribution in Odonata of Britain and Ireland. *PeerJ*, **3**, e1410.

Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009) Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, **15**, 732–743.

R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rice, W.R. (1989) Analysing tables of statistical tests. *Evolution*, **43**, 223–225.

Roslin, T., Várkonyi, G., Koponen, M., Vikberg, V. & Nieminen, M. (2013) Species-area relationships across four trophic levels – decreasing island size truncates food chains. *Ecography*, **37**, 443–453.

Scheper, J., Reemer, M., van Kats, R., Ozinga, W.A., van der Linden, G.T.J., Schaminée, J.H.J., Siepel, H. & Kleijn, D. (2014) Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *PNAS*, **111**, 17552–17557.

Shaw, M.R. & Hochberg, M.E. (2001) The neglect of parasitic Hymenoptera in insect conservation strategies: the British fauna as a prime example. *Journal of Insect Conservation*, **5**, 253–263.

Steffan-Dewenter, I., Klein, A.M., Gaebele, V., Alfert, T. & Tscharntke, T. (2006) Bee diversity and plant–pollinator interactions in fragmented landscapes. *Plant–Pollinator Interactions: From Specialization to Generalization*, pp. 387–407. (ed. by N.M. Waser and J. Ollerton), University of Chicago Press, Chicago, illinois.

Stoate, C., Baldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L. & Ramwell, C. (2009) Ecological impacts of early 21st century agricultural change in Europe – A review. *Journal of Environmental Management*, **91**, 22–46.

Szczepko, K., Kruk, A., Bartos, M. & Wiśniowski, B. (2013) Factors influencing the diversity of cuckoo wasps (Hymenoptera: Chrysididae) in the post-agriculture area of the Kampinos National Park, Poland. *Insect Conservation and Diversity*, **6**, 339–353.

Thomas, J.A. (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360**, 339–357.

Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K. & Kouki, J. (2006) Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. *Annales Zoologici Fennici*, **43**, 373–383.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Williams, N.M., Crone, E.C., Roulston, T.H., Minckley, R.L., Packer, L. & Potts, S.G. (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, **143**, 2280–2291.

Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B. & Kunin, W.E. (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature*, **432**, 393–396.

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